INTERRELATIONSHIPS WITHIN THE ANACANTHOBATIDAE (CHONDRICHTHYES, RAJOIDEA), WITH A DESCRIPTION OF THE LECTOTYPE OF *ANACANTHOBATIS MARMORATUS* VON BONDE & SWART, 1923

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(With 14 figures and 2 tables)

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Introduction

In 1923 Von Bonde & Swart described two new species of skate, *Anacanthobatis marmoratus* and *A. dubius*, from off the coast of Natal, South Africa (the proposed name *Leiobatis* being preoccupied—Errata Slip, Von Bonde & Swart 1923). The species were included in a separate family Anacanthobatidae, which was considered to be part of the Masticura (=Myliobatoidea). Because of this suggested relationship and because of the structure of the teeth and lack of dorsal fins, Barnard (1925), Fowler (1941) and Smith (1961) included the genus in the family Dasyatidae. However, Bigelow & Schroeder (1951, 1953, 1962) and Hulley (1972*a*) consider that the nature of the pelvic fins, the presence of lateral prepelvic processes on the pelvic girdle and the number of proximal basal segments in the clasper preclude their incorporation with the Dasyatidae, and recognize the Anacanthobatidae as a distinct family of the order Rajoidea. This distinction is supported by the typical rajoid egg case in *Anacanthobatis marmoratus* (Wallace 1967).

At present, two genera are recognized within the family, *Anacanthobatis*

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(*A. marmoratus*, *A. longirostris*, *A. americanus*, *A. borneensis*) and *Springeria* (*S. foliorostris*, *S. melanosoma*, *S. ori*), and *A. dubius* is now considered to be a junior synonym of *A. marmoratus* (Bigelow & Schroeder 1962; Wallace 1967). Many of the initial definitive characters for the genus *Springeria* (Bigelow & Schroeder 1951) have fallen away with further taxonomic investigation (Bigelow & Schroeder 1953, 1962; Chan 1965*a*; Wallace 1967), so that the recognition of the genus now rests solely on the terminal leaf-like expansion of the snout.

During the course of investigations on the interrelationships of southern African Rajidae (Hulley 1972*a*), the claspers of *Anacanthobatis marmoratus* and *A. americanus* were briefly examined by the author. Basic major differences in the clasper structure suggested that two genera were possibly involved and that the family Anacanthobatidae, as defined at present, might be diphyletic and have a comparatively early origin (Hulley 1972*a*: fig. 57). However, these conclusions were only tentatively advanced until an investigation could be extended to other anacanthobatid species. This paper represents the results of such an investigation.

Material and Methods

Type specimens of the following species were examined: *Anacanthobatis marmoratus* (RUSI 662), *A. borneensis* (BMNH 1965. 1. 29. 1), *A. longirostris* (USNM 196446), *Springeria melanosoma* (USNM 198121) and *S. ori* (ORI B 187, B 188); and specimens of *A. marmoratus* (ORI B 2, B 3, B 174, B 202), *A. longirostris* (ORE 10827), *A. americanus* (ORE 10602/SAM 26626) and *S. foliorostris* (ORE 10440, 10898) were also examined. X-ray photographs of the type specimen of *Springeria foliorostris* (USNM 152546) were supplied by the United States National Museum.

BMNH=British Museum (Natural History); ORE='Oregon II' Station (material at USNM); ORI=Oceanographic Research Institute, Durban; RUSI=J. L. B. Smith Institute of Ichthyology, Grahamstown; SAM=South African Museum; USNM=United States National Museum.

The structure of the claspers appears to be the most reliable basis on which to interpret interrelationships within the Rajoidea (Ishiyama 1958; Stehmann 1970; Hulley 1970, 1972*a*), so that this method has been employed in the present study. However, *Springeria melanosoma* and *S. ori* are known only from juvenile females, so that additional criteria have been used.

Designation and Description of the Lectotype of *ANACANTHOBATIS MARMORATUS*

The type-species *Anacanthobatis marmoratus* Von Bonde & Swart, 1923 was based on two syntypes, a female (245 mm total length) and a male (238 mm total length) both trawled at 30°09, 45'S, 30°58, 02'E in 292,5 m. These specimens were housed in the collection of the Government Marine Survey, Cape Town. Unfortunately, this collection was later broken up and a large proportion of it was lost to posterity. However, during the preparation of his book *Sea fishes of southern Africa*, a number of specimens from this collection was donated to the late Professor J. L. B. Smith, among which was a single male specimen of *Anacanthobatis marmoratus*. Smith was informed that this specimen was the 'type' (M. M. Smith, personal communication), and it was photographed for inclusion in the book (Smith 1961: fig. 84). The female specimen is missing.

I now designate this male specimen (RUSI 662), housed in the collection of the J. L. B. Smith Institute of Ichthyology, Grahamstown, as the lectotype of the species *Anacanthobatis marmoratus* Von Bonde & Swart, 1923.

Anacanthobatis marmoratus Von Bonde & Swart, 1920

(Fig. 1A, B)

Lectotype

A male (232,9 mm total length), trawled at 30°09, 45'S, 30°58, 02'E in 292,5 m by the S.S. *Pickle* (Station 152); in the collection of the J. L B. Smith Institute of Ichthyology (RUSI 662).

Description

Disc from base of rostral filament about 1,2 times as broad as long, its width 1,5 in total length excluding filament; maximum angle from base of filament to level of spiracles about 102°; end of snout with rostral filament arising from small, bluntly-rounded protuberance; anterior margins of disc concave behind level of protuberance and again at level of spiracles; outer angles rounded; posterior margins evenly convex. Axis of greatest breadth 1,1 times as far from base of filament as from posterior edge of disc. Tail slender, about 2,0 in total length from base of filament, with narrow lateral folds extending to its base.

Skin perfectly naked everywhere and without dermal denticles of any sort, but with 2 rows of hooked alar spines at outer angles of disc.

Snout in front of orbits 3,8 times as long to base of filament as distance between orbits; its length in front of mouth 3,9 times as great as distance between nostrils. Eye 1,7 times as long as spiracles; distance between orbits 1,1 times as great as length of orbit. Rostral cartilage extending to base of rostral filament as hard bar, without a segment; tip of rostral bar forming bluntly-rounded protuberance at base of filament. Anterior rays of pectorals extending almost to rostral appendices.

Mouth slightly arched; nasal curtain fringed; expanded posterior margin of nostril fringed, and overlapping corners of mouth. Teeth arranged in 29 regular rows in upper jaw, with large round bases and laterally directed, sharp, posterior cusps.

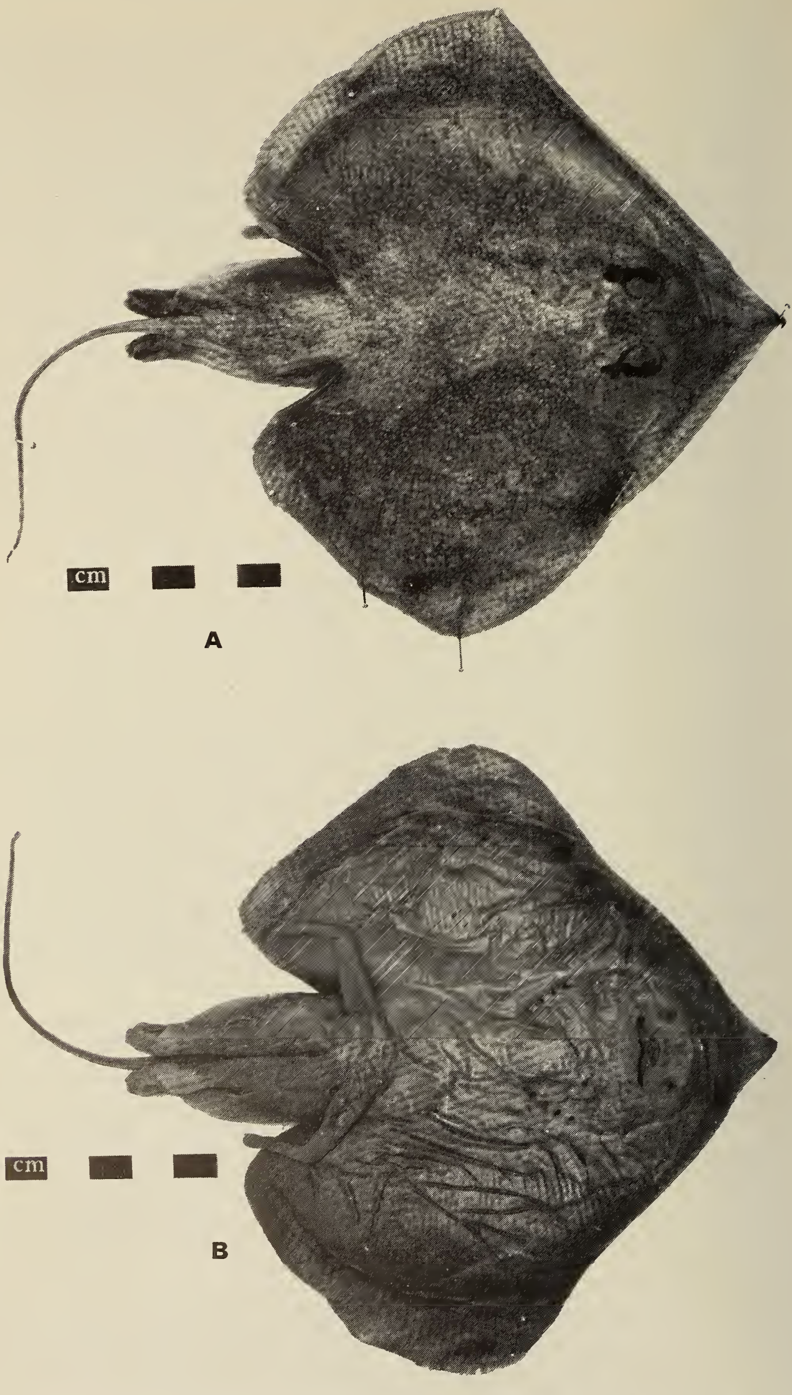

Fig. 1. *Anacanthobatis marmoratus* Von Bonde & Swart. LECTOTYPE (RUSI 662). A. dorsal view; B. ventral view.

TABLE 1

Anacanthobatis marmoratus. (Lectotype.) Measurements expressed in millimetres and as percentage of the total length to base of filament. Figures in parentheses refer to Von Bonde & Swart (1923).

	mm	%
Total length	232,9 (238)	—
Total length to base of filament	230,4	100,0
Length of filament	2,5	1,1
Disc width	152,3 (155)	66,1
Disc length	130,7	56,7
Snout to greatest disc width	69,5	30,2
Snout to axils of pelvics	94,5	41,0
Snout length: in front of orbits	31,1	13,5
in front of mouth	31,5	13,6
in front of nostrils	26,6	11,5
Eye: horizontal diameter	7,4	3,2
distance between eyes	8,1	3,5
Spiracle: length	4,5	1,9
distance between spiracles	19,6	8,5
Mouth: width	15,4	6,7
Nostrils: distance between inner ends	14,6	6,3
Gill slits: length 1st	2,1	0,9
3rd	2,6	1,1
5th	2,0	0,9
distance between 1st	28,6	12,4
5th	15,8	6,9
Pelvics: length anterior margin	36,0	15,6
length posterior margin	32,4	14,1
base width	8,2	3,6
Caudal fin: upper base length	17,2	7,4
lower base length	9,6	4,1
Snout to middle of vent	111,2	48,3
Middle of vent to tip of tail	119,2 (123)	51,7

Pelvics divided into slender, limb-like, anterior lobe, arising separately from ventral surface of disc, and posterior, fin-like lobe. Posterior lobe free from inner pectoral margin, but posterior margin joined to tail almost to tip of fin.

Dorsal fins absent. Caudal fin membraneous, with epiural lobe larger than hypural lobe.

Colour (in alcohol): dorsal surface irregularly mottled light brown and white, with scattered ocelli; papillae and rostral filament dark brown. Ventral surface uniformally pale.

PELVIC GIRDLE

The pelvic girdles of *Anacanthobatis marmoratus* and *A. americanus* have been described by Hulley (1972*a*).

In all Rajoidea, the pelvic girdle consists of a simple transverse bar, which is expanded at the iliac regions and possesses a pair of anteriorly-directed, lateral prepelvic processes. Paired iliac processes arise posteriorly from the iliac region, but recurve dorsally to terminate as blunt processes.

The pelvic girdle in the Anacanthobatidae (Fig. 2) is typically U-shaped

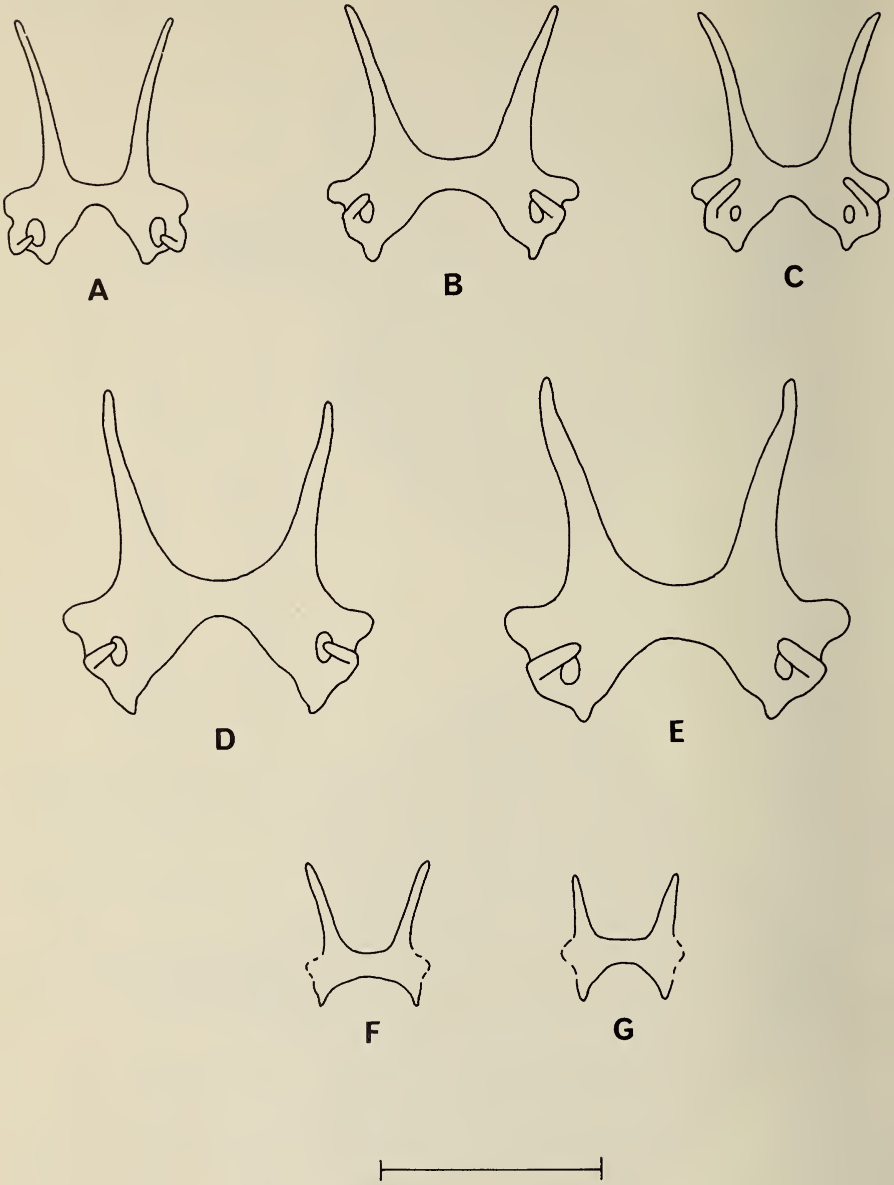

Fig. 2. Pelvic girdles of the Anacanthobatidae. A. *Anacanthobatis marmoratus* (♂); B. *A. borneensis* (♂); C. *A. americanus* (♂); D. *A. longirostris* (♂); E. *Springeria foliorostris* (♂); F. *S. ori* (♀); G. *S. melanosoma* (♀). Scale 20 mm.

with the iliac regions considerably more developed than in the Rajidae, and possesses elongate prepelvic processes. These appear to serve only for the attachment of the abdominal musculature and have no relationship to the musculature of the anterior, limb-like lobe of the pelvic fin. The three groups of muscles which are responsible for dorso-ventral movement of the anterior lobe (ventral muscles of the marginal ray—Frechkop 1925) insert at the bases of the prepelvic processes. The comparative lengths of the prepelvic processes vary considerably: *Anacanthobatis marmoratus* (0,6–0,8 times the girdle width); *A. longirostris* (0,6–0,7); *A. americanus* (0,8); *A. borneensis* (0,6); *Springeria foliorostris* (0,6–0,8); *S. ori* (0,8); and *S. melanosoma* (0,5). In all species, the processes project laterally, except in *Anacanthobatis longirostris* and *Springeria foliorostris* (Fig. 2), in which the distal extremities recurve medially.

There is a single, large obturatorial foramen on each side in all species. Sexual dimorphism is exhibited by the girdle, so that the girdle in females has a comparatively longer ischio-pubic bar. This is probably associated with the oviparous behaviour of the family.

Rostral Filament and Terminal Expansion

The rostral filament and terminal expansion of the snout of all described anacanthobatid species are illustrated in Figure 3. The rostral filament, which varies in length intraspecifically, arises from a small, bluntly-rounded protuberance at the anterior extremity of the snout. This protuberance is found in all species and should not be confused with the terminal leaf-like expansion of the snout in *Springeria foliorostris* (Fig. 3E). In this species, the anterior margins of the disc are markedly constricted against the rostral bar some little distance behind the protuberance, so as to encompass the rostral appendices, i.e. the appendices themselves form the expansion. This is not found in either *Springeria ori* or *S. melanosoma* (Figs 3F, G). In these species, only a blunt anterior protuberance is present. This is formed by the anterior extremity of the rostral bar in relation to the leading edges of the rostral appendices, and has its counterpart in all other species of the genus *Anacanthobatis* (Fig. 3).

Pectoral and Pelvic Fin Radials

Quignard (1965) and Stehmann (1970) have discussed the distribution of pectoral fin radials in the Rajidae and the taxonomic value of the total number of radials in each wing. It appears that while the distribution of pectoral radials may vary intraspecifically and may even vary on opposite sides of the same individual, the total count may, in some cases be used to distinguish between closely related species, e.g. *Raja oxyrhynchus* and *R. nidarosiensis*. Furthermore, it appears that this criterion may even be valid at the subgeneric level in certain instances, e.g. *Raja alba* (Stehmann 1970: fig. 13). However, Stehmann (1970) points out that in general natural combinations

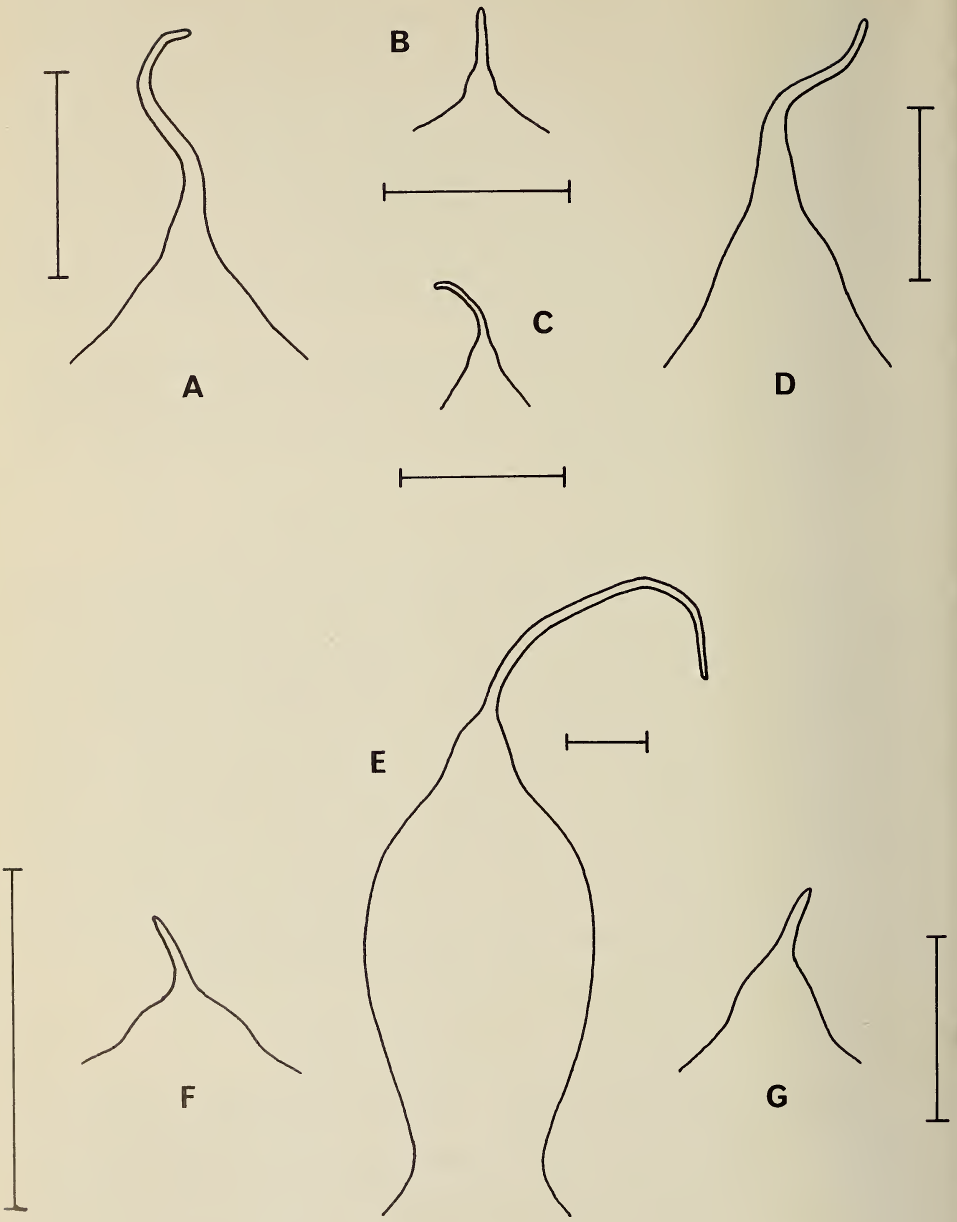

Fig. 3. Rostral filament and terminal expansion of the Anacanthobatidae. *A. Anacanthobatis marmoratus*; B. *A. americanus*; C. *A. borneensis*; D. *A. longirostris*; E. *Springeria foliorostris*; F. *S. melanosoma*; G. *S. ori*. Scale 5 mm.

of species cannot be recognized by mean values of the count.

To assess the value of this method in the Anacanthobatidae, pectoral and pelvic fin radial counts were made from X-ray photographs. The results are presented in Table 2. Since there is no overlap of the pectoral and pelvic fins, direct counts could be obtained from the plates. This method could not be applied to *Springeria melanosoma* and to certain counts in *S. ori*, due to the poor degree of calcification of the radial cartilages.

TABLE 2

Pectoral and pelvic radials in the Anacanthobatidae.

Species	No. Specimens	Total Pectoral	No. Mesopterygial	No. Intercalary	Total Pelvic
A. marmoratus ..	5	72–78	3–5	11–13	13–18
A. borneensis ..	1	75	4	15	14
A. longirostris ..	2	88–90	4–5	16–19	14–19
A. americanus ..	1	66	3	11	12
S. foliorostris ..	3	87–89	6	16–18	16–19
S. ori	1	70	—	—	13–14

CLASPER STRUCTURE

A description of the external and internal structure of the claspers of *Anacanthobatis marmoratus* and *A. americanus* has already been given (Hulley 1972*a*). The terminology of the various components and cartilages of the species examined in this paper are in accordance with the definitions given by Hulley (1972*a*). However, a further term, palp, is now defined:

palp

> A fleshy pad, situated in the dorsal lobe of the clasper glans at about the level of the hypopyle, and lying along the outer lateral margin of the closed glans: with or without a distal filament; the internal support provided by the distal projection of the dorsal marginal cartilage.

It should be noted that the component usually associated with the distal projection of the dorsal marginal is the pseudorhipidion. However, the distinction between these two components has been made because the pseudorhipidion extends distally and medially in the glans as a sharp-edged cartilaginous tongue while the palp extends distally and laterally as a well-developed fleshy pad, not unlike the foot of a bivalve mollusc. Furthermore, in species in which the pseudorhipidion is present, the rhipidion is absent, the probable function of the pseudorhipidion being to spread the ejaculating spermatozoa (Leigh-Sharpe 1920). But anacanthobatids which possess a palp, also possess a rhipidion, indicating a different function for the palp and pseudorhipidion.

Springeria foliorostris (Figs 4, 5, 6)

Claspers comparatively short and naked, with slightly expanded glans more or less dorso-ventrally flattened and pointed; pseudosiphon absent; spur well developed, forming, together with palp, the outer lateral margin of dorsal

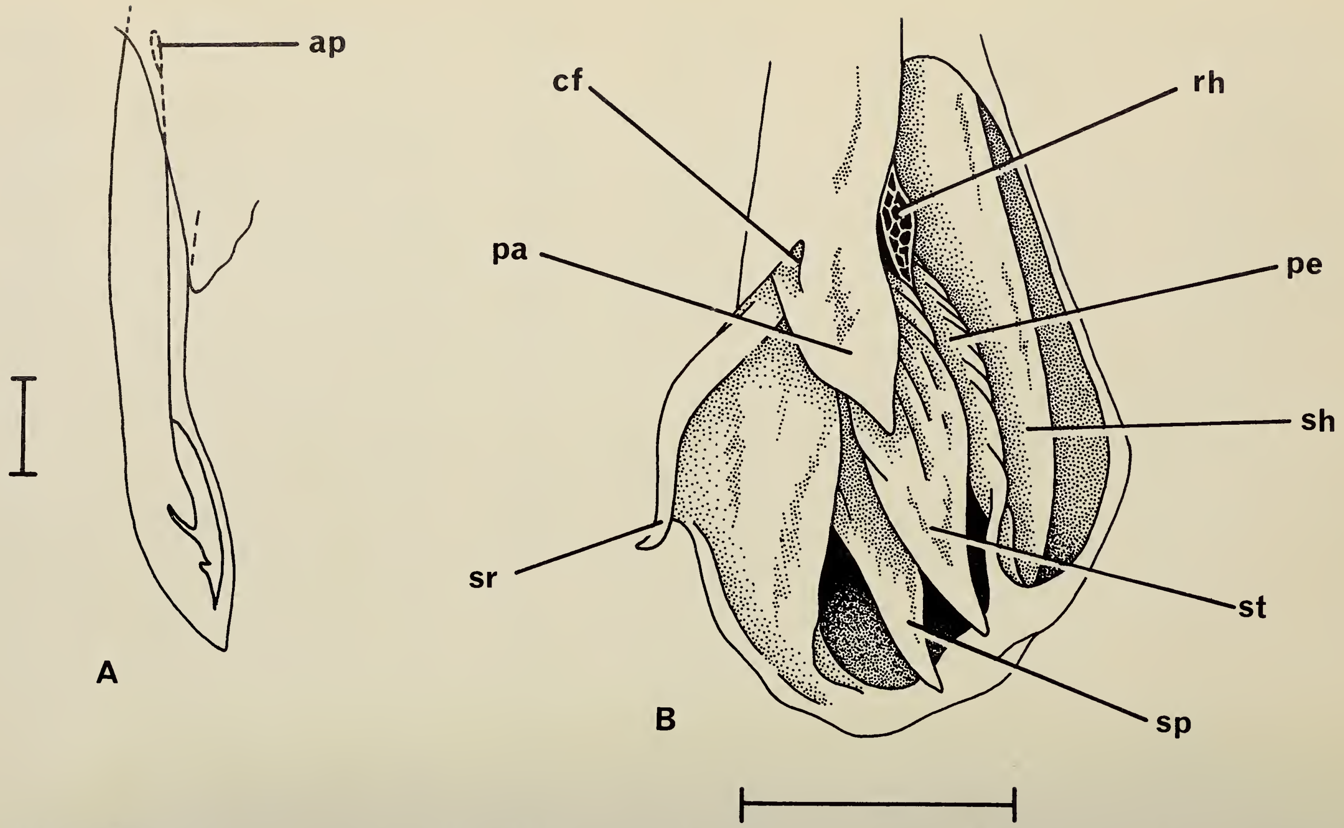

Fig. 4. *Springeria foliorostris*. A. external view of right clasper from dorsal side; B. lateral view of right clasper opened to show structural features of the glans. Scale 10 mm.

ap—apopyle; cf—cleft; pa—palp; pe—pent; rh—rhipidion; sh—shield; sp—spike; sr—spur; st—sentinel.

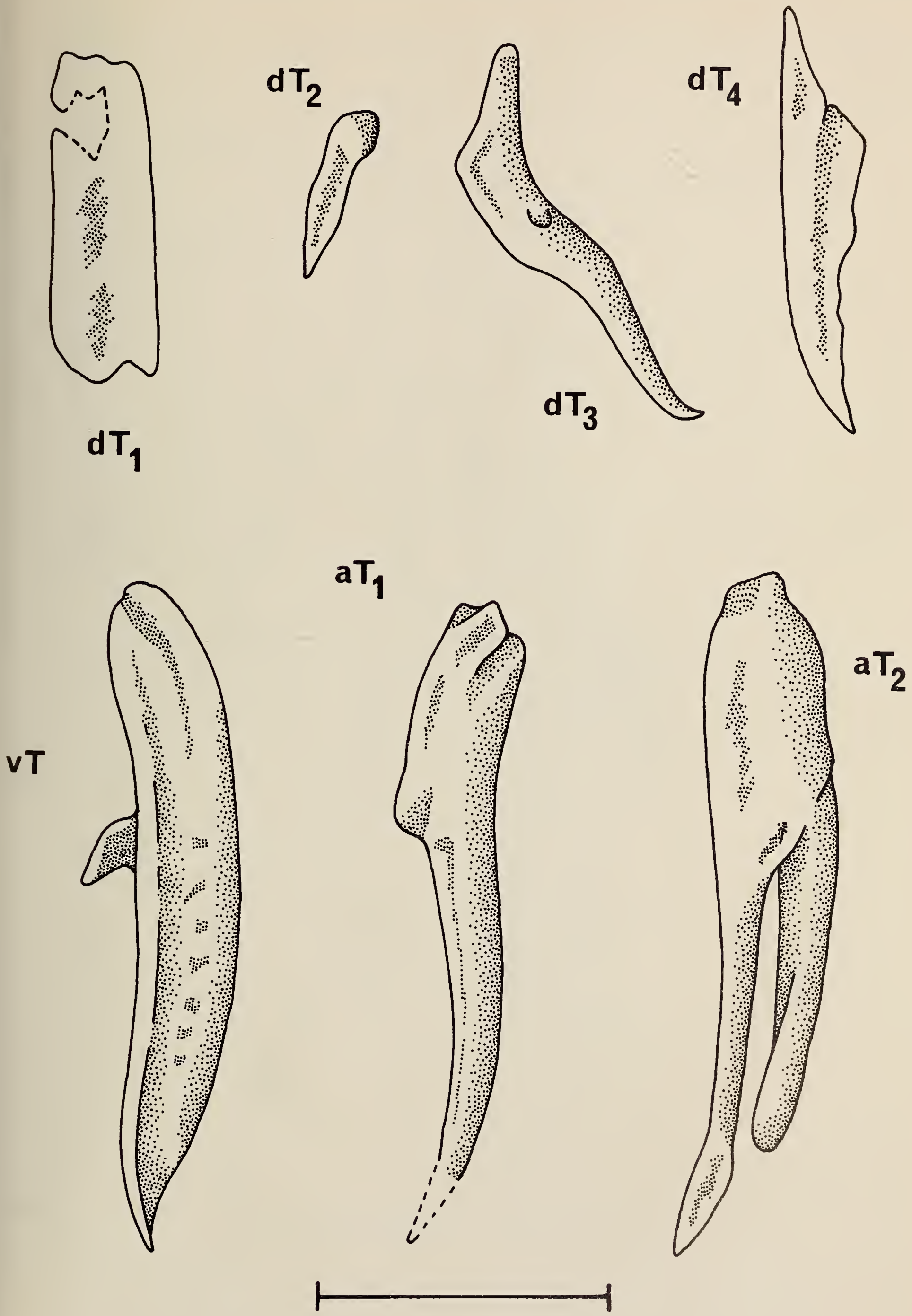

Fig. 5. *Springeria foliorostris*. Terminal cartilages of the right clasper. dT$_1$, dT$_2$, dT$_3$, dT$_4$, vT—dorsal view; aT$_1$, aT$_2$—ventral view. Scale 10 mm.

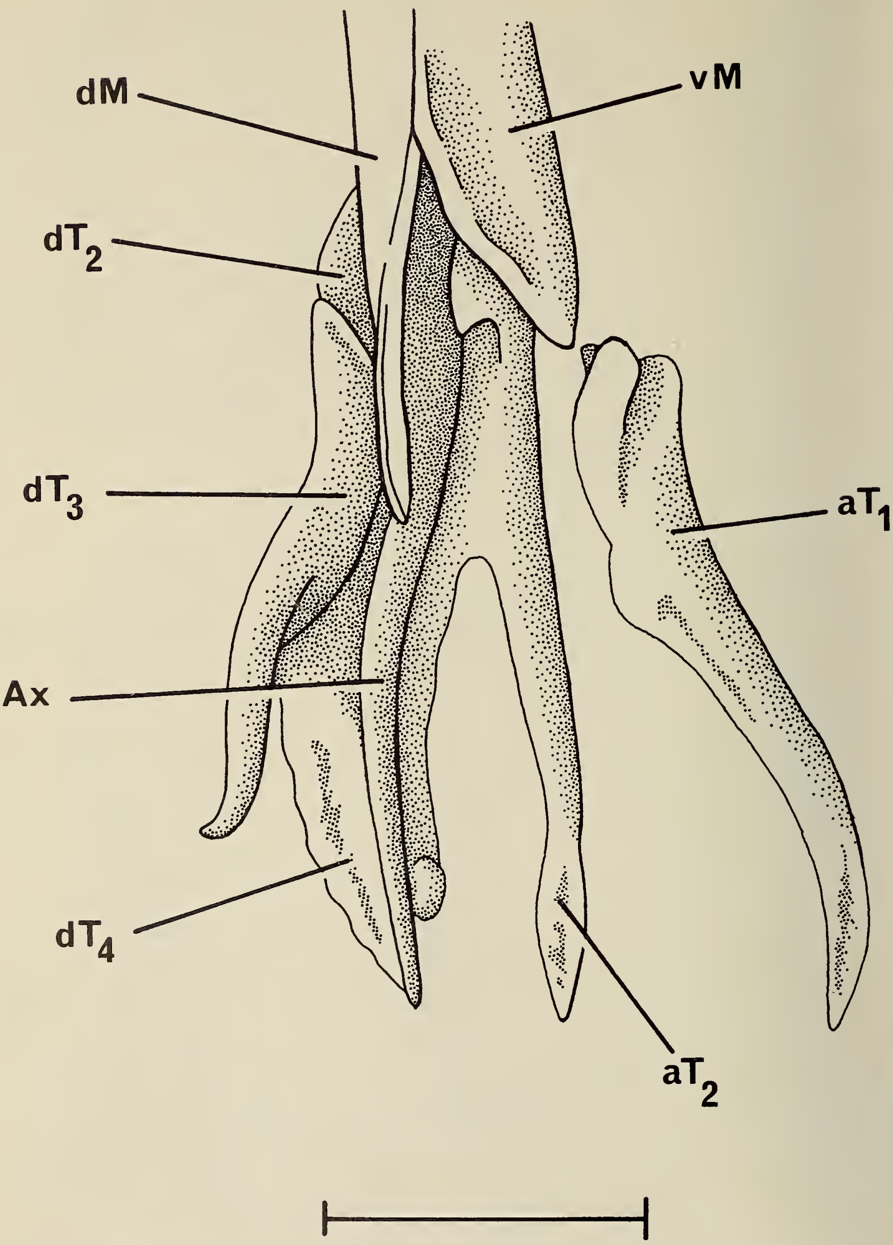

Fig. 6. *Springeria foliorostris.* Cartilages of right clasper with dT$_1$ and vT removed. Scale 10 mm.

lobe; inner dorsal lobe with proximal cleft and large fleshy palp, without a distal filament; rhipidion at level of hypopyle with pent extending distally from the rhipidion along inner lateral margin of shield; sentinel well developed and covered with pleated epithelia, partially covering spike; sentinel and spike situated medially.

Proximal cartilaginous elements (basal group): b_1 and b_2 cartilages, with covering β-cartilage arising from stepped axial to about one-half the length of the b_1-cartilage. Four dorsal terminal cartilages: dT_1 plate-like, without a proximal shelf, situated entirely on dorsal side of organ, poorly calcified proximally; dT_2 comparatively small and connecting dM with dT_3; dT_3 well developed and projecting laterally outwards as a sharp point, the spur; dT_4 flat and poorly calcified, bonded to outer lateral edge of pointed Ax. vT dorsally concave with pointed distal tip and short anterior notch at about half the length of the cartilage. aT_1 comparatively narrow and elongate, with sharp-pointed, dorso-ventrally flattened tip. Bifurcate aT_2, with spinal projection extending distally to a somewhat expanded, dorso-ventrally flattened blade-like tip, and with well developed attachment process arising at about one-third the length of the cartilage and tightly bonded to lateral edge of Ax.

Anacanthobatis longirostris (Figs 7, 8, 9)

Clasper comparatively short with naked, slightly expanded and dorso-ventrally flattened tip; pseudosiphon absent; spur well developed, forming outer lateral margin of dorsal lobe with palp; inner dorsal lobe with proximal cleft; slender palp arising at level of rhipidion, with a short distal filament; rhipidion at level of hypopyle, without a pent; shield dorsally convex and distally truncate, without laminate integument; sentinel with sharp point and covered basally with pleated integument, partially overlying spike; sentinel and spike situated medially.

Proximal cartilaginous elements (basal group): b_1 and b_2 cartilages with dorsally situated β-cartilage, arising from stepped Ax to about one-half the length of b_1-cartilage. Four dorsal terminal cartilages: dT_1 without proximal shelf but with distal point, situated dorsally but with inner lateral edge curved to wrap around Ax on to ventral side; dT_2 comparatively small and comma-shaped, connecting dM with dT_3; dT_3 asymmetrical proximally and broadly expanded distally, with sharp-pointed, Z-shaped outer lateral projection, the spur, and short, truncate, inner lateral extension; dT_4 shield-like and poorly calcified, with proximal inner extension fusing with dT_3. vT simple, dorsally convex with truncate distal tip and with short anterior notch at about one-half the length of the cartilage. aT_1 dorso-ventrally flattened with condyle-like proximal end and slightly expanded, knife-like distal point. Bifurcate aT_2, with spinal projection extending distally to somewhat expanded, dorso-ventrally flattened, blade-like tip, and with well developed attachment process, arising at about one-third the length of the cartilage, tightly bonded to lateral edge of Ax.

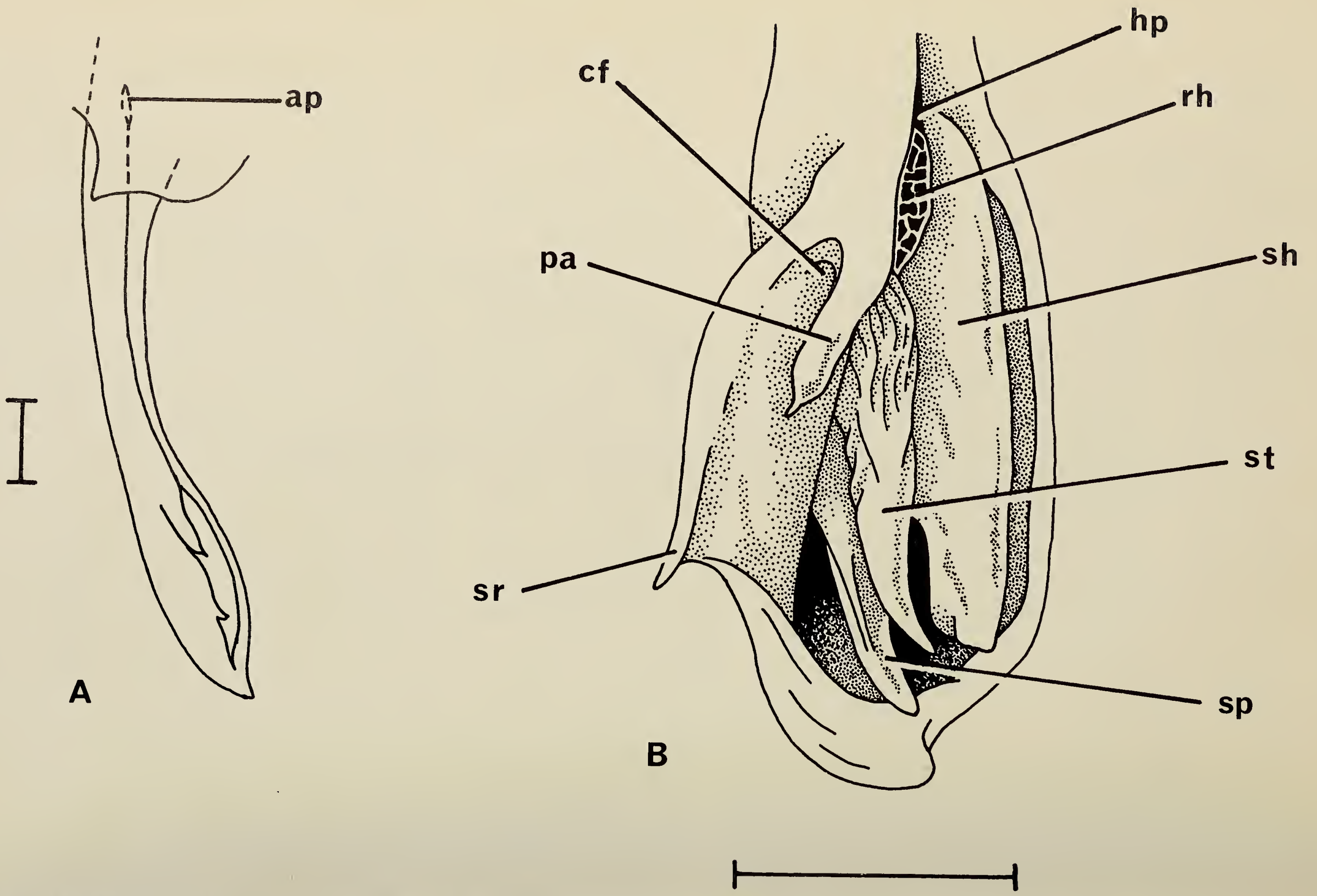

Fig. 7. *Anacanthobatis longirostris*. A. external view of right clasper from the dorsal side. B. lateral view of right clasper opened to show structural features of the glans. Scale 10 mm.
ap—apopyle; cf—cleft; hp—hypopyle; rh—rhipidion; pa—palp; sh—shield; sp—spike; sr—spur; st—sentinel.

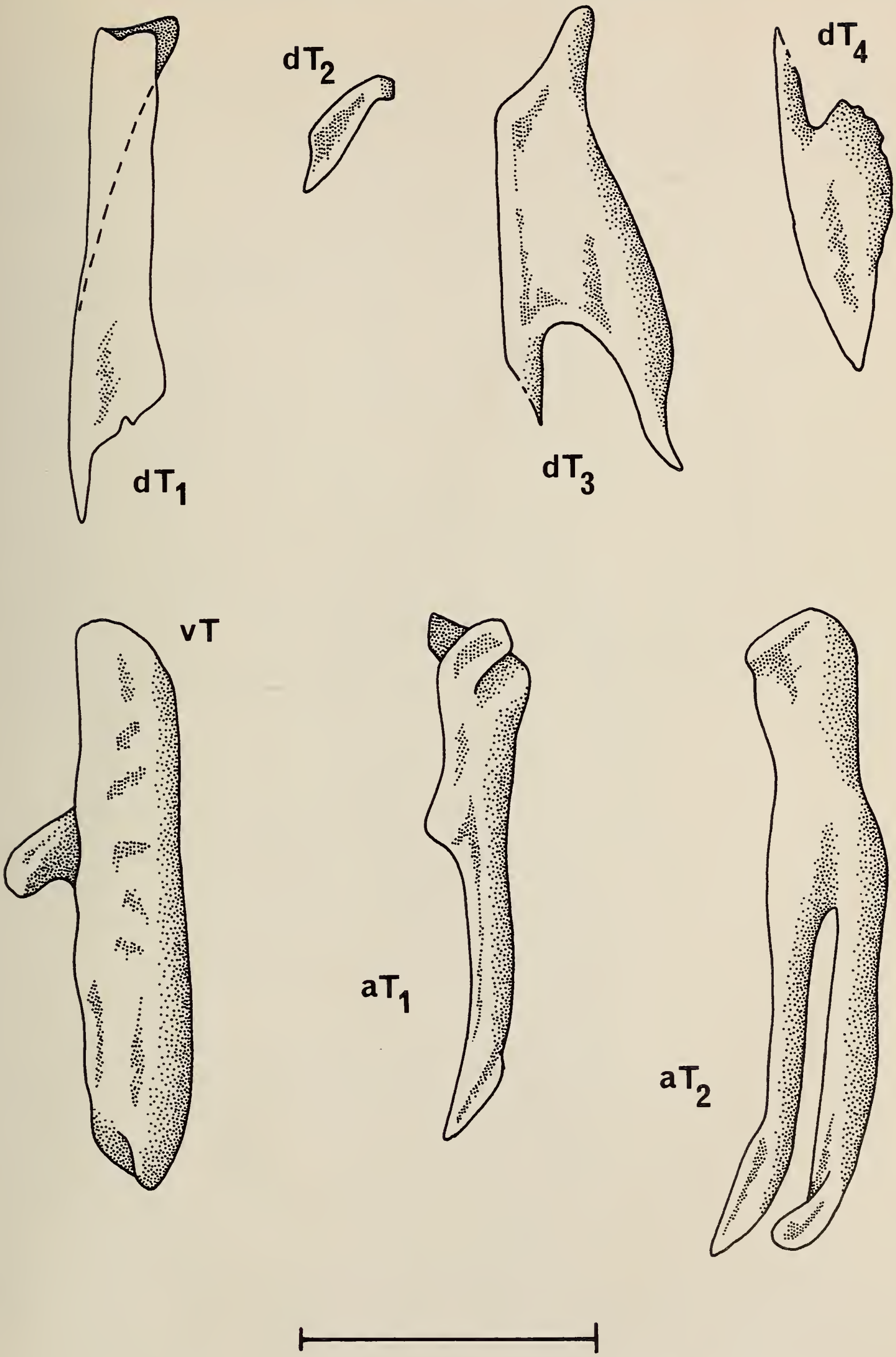

Fig. 8. *Anacanthobatis longirostris*. Terminal cartilages of the right clasper. dT_1, dT_2, dT_3, dT_4, vT—dorsal view; aT_1, aT_2—ventral view. Scale 10 mm.

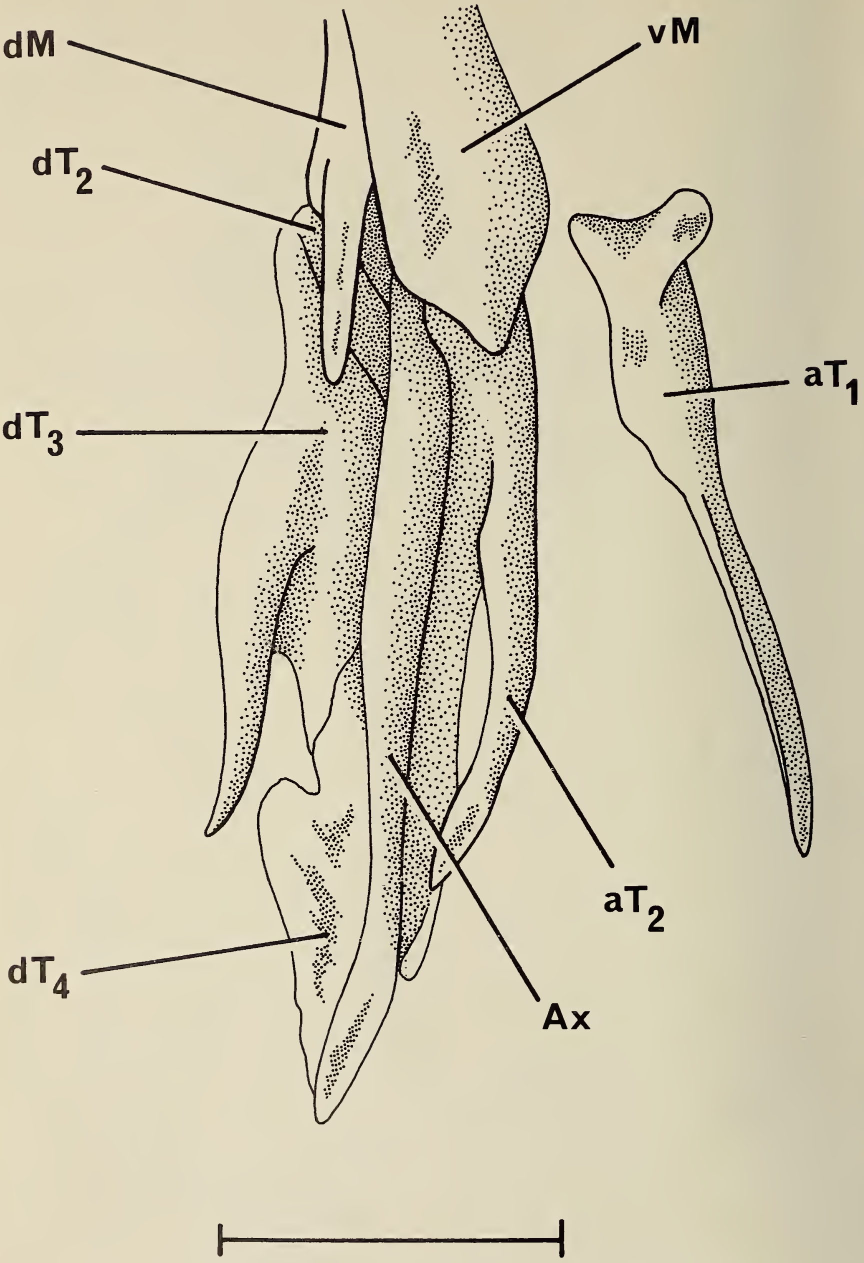

Fig. 9. *Anacanthobatis longirostris*. Cartilage of right clasper with dT$_1$ and vT removed. Scale 10 mm.

Anacanthobatis borneensis (Figs 10, 11, 12)

Claspers short with naked, slightly expanded and dorso-ventrally flattened glans; pseudosiphon, spur and palp absent; inner dorsal lobe with 2 proximal clefts; rhipidion at level of hypopyle; shield small, without pent; sentinel and, spike similar in size and shape, with dorso-ventrally flattened, blade-like tips situated laterally in glans; sentinel capable of rotation.

Proximal cartilaginous elements (basal group): b_1 and b_2 cartilages with dorsally situated β-cartilage arising from stepped Ax almost to b_1/basipterygium junction. Two dorsal terminal cartilages: dT_1 absent, the *m. dilatator* inserting at proximal region of dT_3; dT_2 small and comma-shaped joining dT_3 with dM; dT_3 asymmetrical proximally with a small window, and distally elongated to form a straight, flat, lateral extension, which does not develop into a spur; short, inner lateral extension of dT_3 loosely connected with pointed Ax; dT_4 absent. vT expanded proximally to form a short shield, with elongate anterior notch situated at about one-third the length of the cartilage and wrapping around inner lateral margin of the organ on to the dorsal side; distal extremity of vT pointed and curving laterally inwards. Simply-pointed aT_1 with expanded joint-like proximal region. aT_2 asymmetrical, spinal process slightly Z-shaped with dorso-ventrally flattened blade-like tip; attachment process small and only slightly calcified, arising at about one-quarter the length of the cartilage and loosely bonded to lateral edge of Ax.

Discussion

Consideration should be given to the fact that the number of species in the family Anacanthobatidae is small, so that further division into subgeneric groupings does not appear to serve a useful taxonomic purpose. However, within the Rajoidea, such subdivision serves not only for taxonomy but may also be employed in the construction and interpretation of phyletic relationships. It is within this context that the subgenera within the Anacanthobatidae will be considered.

There can be no doubt that a single family is involved in the cases of all described anacanthobatid species. All possess the U-shaped pelvic girdle characteristic of the Anacanthobatidae (Hulley 1972*a*). Furthermore, there are two proximal segments in the basal group of the clasper cartilages, which together with the presence of a pair of lateral prepelvic processes on the pelvic girdle, fully substantiate the inclusion of the family within the Rajoidea.

As already stated, the recognition of the genus *Springeria* is based solely on the terminal leaf-like expansion of the snout. The interpretation of this feature does not now appear to have been constant among the various authors of species in this genus (Bigelow & Schroeder 1951; Chan 1965*a*; Wallace 1967). The terminal expansion in *Springeria foliorostris* is well marked and is formed in an entirely different manner to the 'terminal expansion' in either *S. ori* or *S. melanosoma*. In these species, there is merely a blunt protuberance at the base

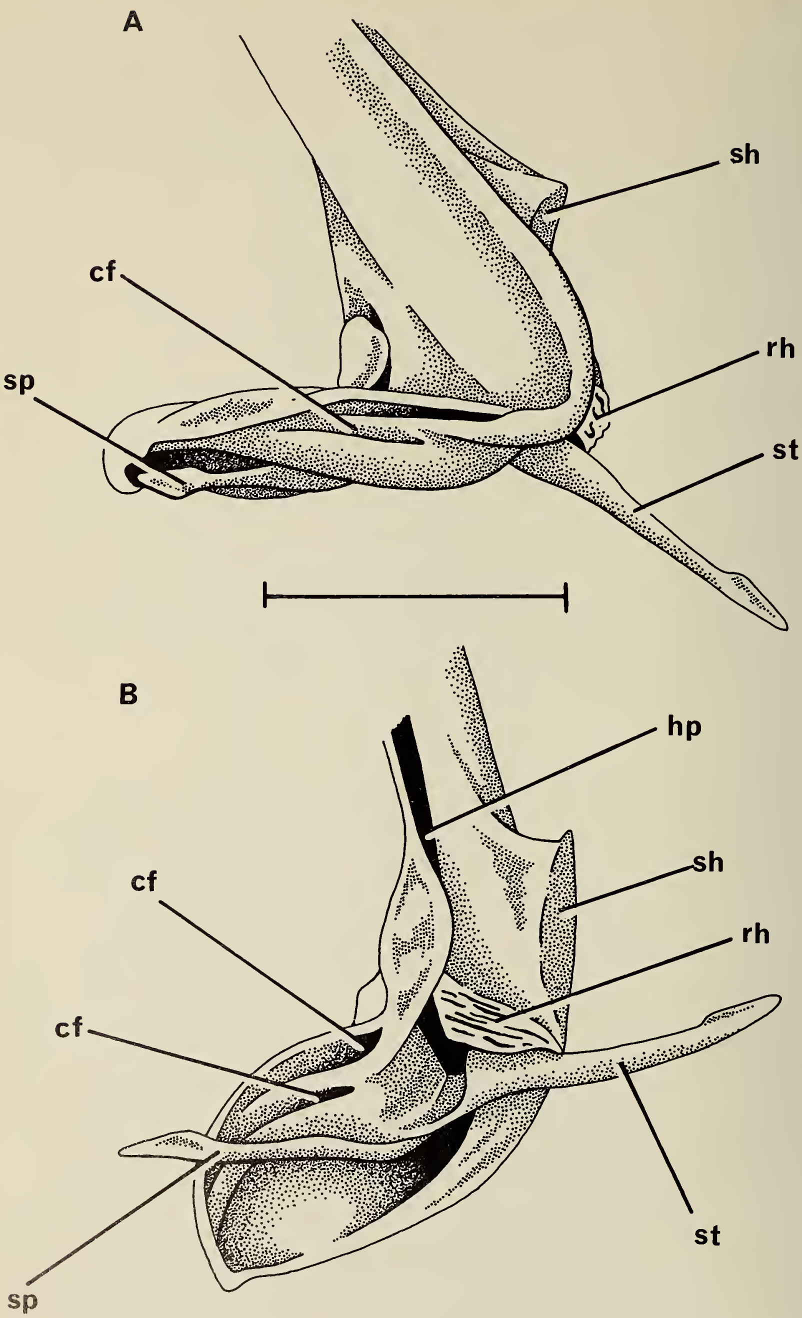

Fig. 10. *Anacanthobatis borneensis*. A. dorsal view of right clasper. B. lateral view of right clasper opened to show structural features of the glans. Scale 10 mm.
cf—cleft; hp—hypopyle; rh—rhipidion; sh—shield; sp—spur; st—sentinel.

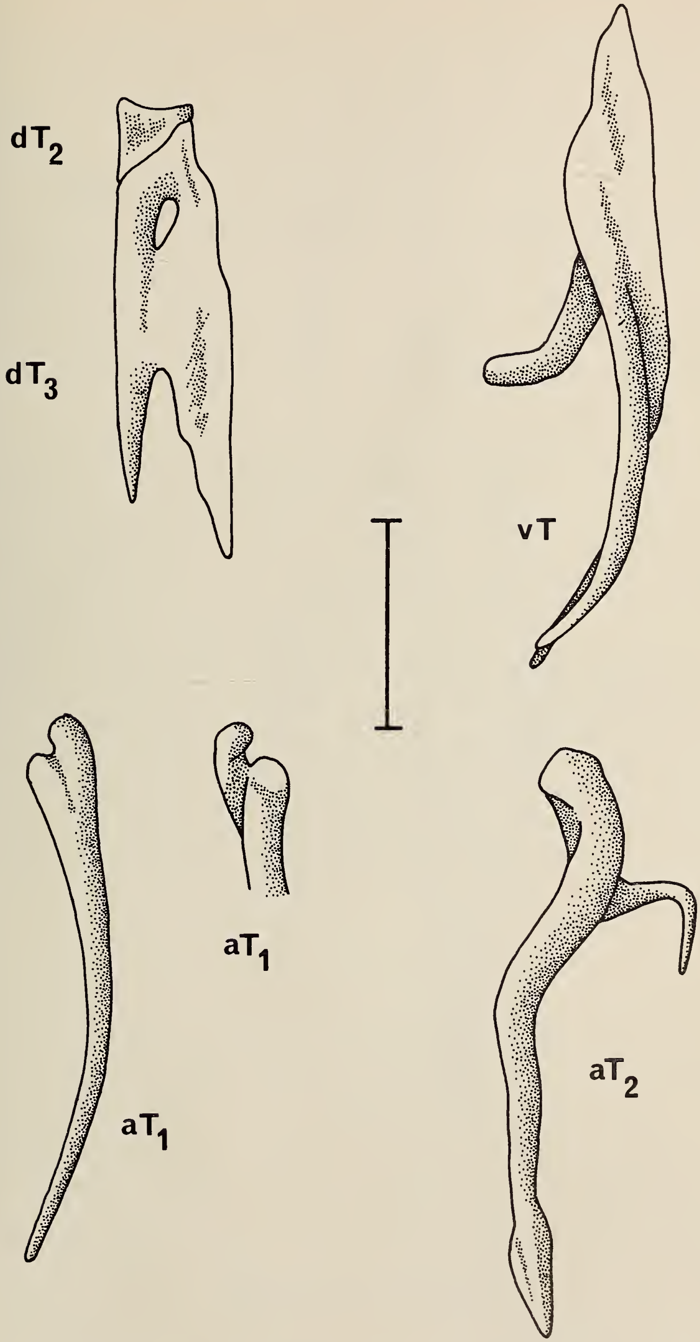

Fig. 11. *Anacanthobatis borneensis.* Terminal cartilages of the right clasper. dT_2, dT_3, vT, aT_1 (head only)—dorsal view; aT_1 (complete) aT_2—ventral view. Scale 5 mm.

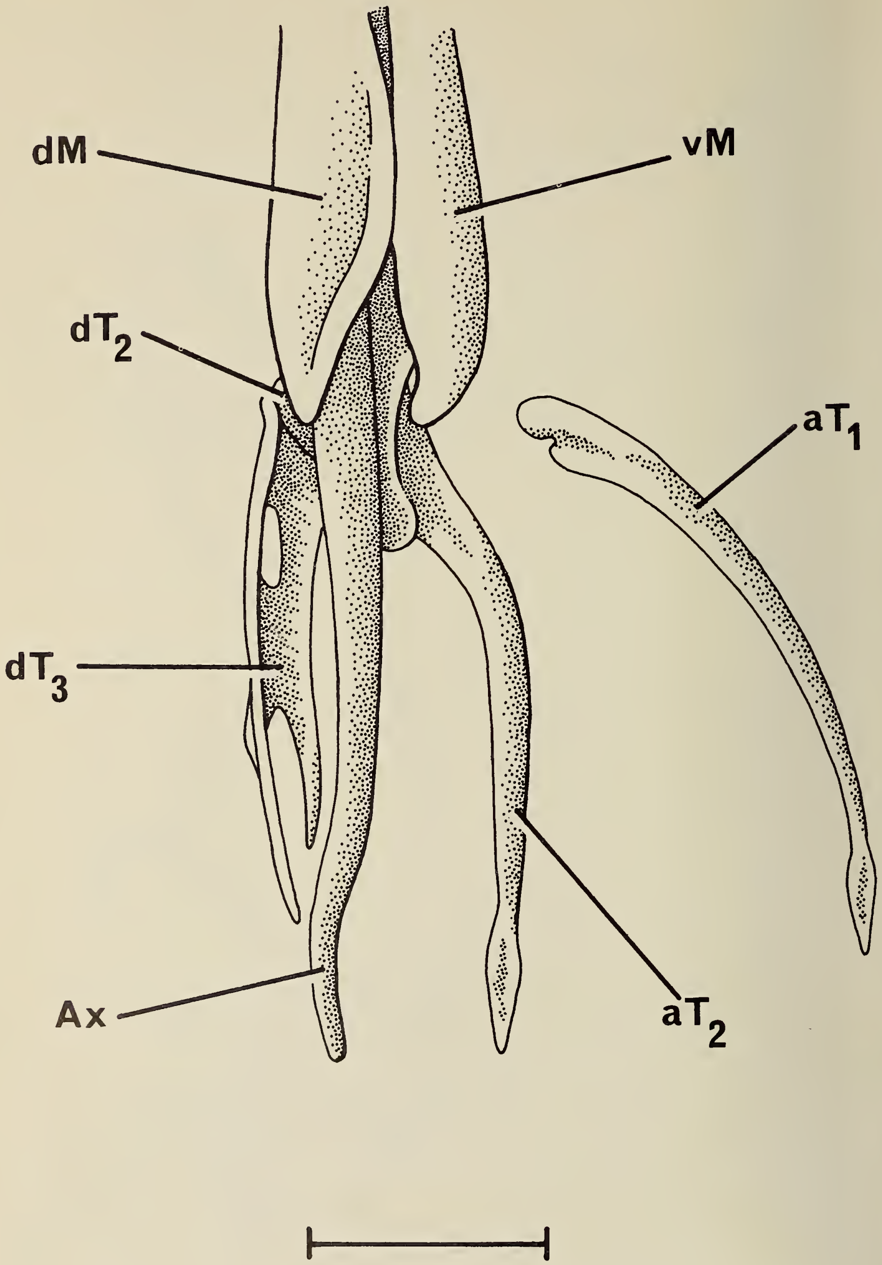

Fig. 12. *Anacanthobatis borneensis*. Cartilages of right clasper with vT only removed. Scale 5 mm.

of the rostral filament, a condition which is approximated in all anacanthobatid species including *S. foliorostris*. These facts, when considered in the light of the similarity in clasper structure of *Springeria foliorostris* and *Anacanthobatis longirostris* (Figs 4–9), indicate that the genus *Springeria* as based on this character is invalid, and that a terminal leaf-like expansion of the snout is a character applicable only at the species level to *S. foliorostris*.

This conclusion is further supported by the fact that the number of radials in both the pectoral and pelvic fins does not allow for the separation of *Springeria* as a separate genus. It appears that the number of mesopterygial radials in *Springeria foliorostris* is slightly higher than in other *Anacanthobatis* species. Unfortunately, counts of the number of mesopterygial radials in *S. ori* and *S. melanosoma* were not possible, due to the small degree of calcification of these cartilages.

X-ray examination has shown that unlike the Rajidae, the pectoral girdle in the Anacanthobatidae is sexually dimorphic. In males the propterygium consists of two articulated segments, while in females there is a single propterygial element (Fig. 13). In rajids two articulated propterygial elements are found in both sexes. The comparative size of the mesopterygium varies in different species, but its use as a specific, subgeneric or generic diagnostic character is difficult to assess at this stage.

To summarize, the genus *Springeria* cannot be distinguished from *Anacanthobatis*; the terminal leaf-like expansion of the snout is applicable only to *S. foliorostris* and lends itself as a diagnostic character at the species level.

On the basis of the external and internal anatomy of the claspers, the characters of which appear to be the most reliable criteria in the taxonomy of the Rajoidea, the following species of *Anacanthobatis* are now distinguished: *A. marmoratus*, *A. americanus*, *A. longirostris*, *A. borneensis* and *A. foliorostris*.

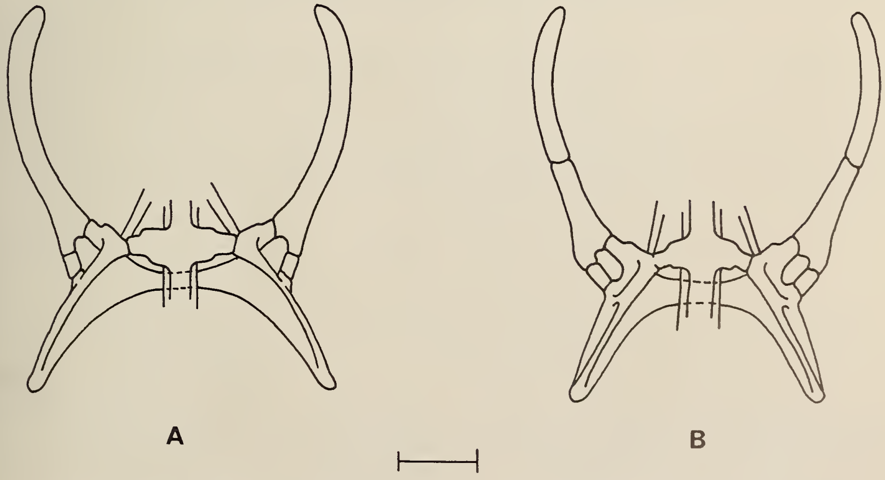

Fig. 13. Pectoral girdles of *Anacanthobatis marmoratus*. A. female; B. male. Scale 10 mm.

Anacanthobatis ori appears to resemble *A. marmoratus* in the complete fusion of the inner margin of the pelvic fin with the base of the tail, a character which is unique to these two species. However, for the moment, *Anacanthobatis ori* is retained as a separate species on the basis of a lower teeth count (20–24 rows in upper jaw in *A. ori*; 32–35 rows in *A. marmoratus*), a comparatively longer and more slender tail, larger eyes (which Wallace (1967) associates with the light intensity of a shallower depth habitat) and a nasal curtain which does not overlap the corners of the mouth. Similarly, *A. melanosomus* is retained for the moment as a separate species to the sympatric *A. borneensis* because of differences in the disc shape, snout length, tail length, nasal curtain and presence of minute thorns along the midline of the base of the tail (Chan 1965*a*, *b*). It should be noted that there is no difference in teeth count in these two species (24 rows in upper jaw). The low value of 14 rows in *A. melanosomus* reported by Chan (1965*a*) arises because the teeth are arranged in quincunx, but are widely separated. Since adult males of *Anacanthobatis ori* and *A. melanosomus* are unknown, it is impossible to comment on them further.

KEY TO SPECIES

1 (a) Dorsal surface of disc with dermal papillae 2
(b) Dorsal surface of disc without dermal papillae 5
2 (a) Pelvics completely fused along entire length with root of tail 3
(b) Pelvics not completely fused along entire length with root of tail 4
3 (a) 20–24 rows of teeth in upper jaw; nasal curtain not overlapping corners of mouth *A. ori*
(b) 32–35 rows of teeth in upper jaw; nasal curtain overlapping corners of mouth *A. marmoratus*
4 (a) Length of tail from middle of vent greater than distance from middle of vent to base of rostral filament; interorbit about 3 in snout length to base of filament *A. melanosomus*
(b) Length of tail from middle of vent less than distance from middle of vent to base of rostral filament; interorbit about 7 in snout length to base of filament *A. borneensis*
5 (a) Length of snout about 4–5 times as long as diameter of eye . . . *A. americanus*
(b) Length of snout about 7–9 times as long as diameter of eye 6
6 (a) Snout with terminal leaf-like expansion; length of tail from middle of vent greater than distance from middle of vent to tip of snout . . . . *A. foliorostris*
(b) Snout without terminal leaf-like expansion; length of tail from middle of vent less than distance from middle of vent to tip of snout . . . . *A. longirostris*

TAXONOMIC ARRANGEMENT OF THE ANACANTHOBATIDAE

On the basis of clasper structure, the family Anacanthobatidae can be taxonomically arranged as follows. It should be noted however that Hulley (1972*a*) has erroneously confused the sentinel/spike and aT_1/aT_2 in *Anacanthobatis americanus*.

Family **Anacanthobatidae**

Genus *Anacanthobatis* Von Bonde & Swart, 1923

type-species *Anacanthobatis marmoratus* Von Bonde & Swart, 1923

1. subgenus *Anacanthobatis* Von Bonde & Swart, 1923
   type-species *Anacanthobatis marmoratus* Von Bonde & Swart, 1923
   species: (?) *Anacanthobatis ori* (Wallace, 1967)—no adult male

Definition

Claspers comparatively small, with spur on lateral dorsal border, but without pseudosiphon; inner dorsal lobe with proximal cleft and with slender proximal palp; palp without a terminal filament; rhipidion present; shield prominent with well developed eperon; sentinel and spike medially positioned; Ax spatulate; three dT elements, with spur developed from dT_3; vT proximally pointed with serrate outer lateral margin and with anterior notch well developed from windowed inner lateral margin; aT_1 distally spoon-shaped; aT_2 simply-pointed, attachment process absent.

2. subgenus *Springeria* Bigelow & Schroeder, 1951
   type-species *Anacanthobatis foliorostris* (Bigelow & Schroeder, 1951)
   species: *Anacanthobatis longirostris* Bigelow & Schroeder, 1962

In accordance with Article 67k of the International Code of Zoological Nomenclature, the name *Springeria* is retained, but is now redefined.

Definition

Claspers comparatively small, with spur developed on lateral dorsal margin but without pseudosiphon; inner dorsal lobe with proximal cleft and with proximal palp; palp with or without a distal filament; rhipidion present; shield well developed, eperon absent but pent present or absent; sentinel and spike positioned medially; Ax with pointed distal extremity; four dT elements, with spur developed from dT_3; vT simple and rounded proximally, with small anterior notch; aT_1 distally pointed or slightly blade-like; aT_2 with well developed blade-like spinal projection and well developed attachment process.

3. subgenus ***Sinobatis*** n. subgen.
   type-species *Anacanthobatis borneensis* Chan, 1965
   species: (?) *Anacanthobatis melanosomus* (Chan, 1965)—no adult male

Definition

Claspers small, without spur on dorsal lateral margin and without pseudosiphon; inner dorsal lobe without palp but with two proximal clefts; rhipidion present; shield poorly developed laterally, but expanded medially to wrap around Ax stem as small dorsal bump; sentinel and spike simple, with slight blade-like distal ends, situated laterally with sentinel capable of rotation; two dT cartilages, but dT_1 absent; spur not developed from distal projection of dT_3; Ax simply pointed distally; aT_1 simple with blade-like end; aT_2 with slender spinal projection and poorly developed attachment process.

4. subgenus ***Schroederobatis*** n. subgen.

type-species *Anacanthobatis americanus* Bigelow & Schroeder, 1962

Definition

Claspers small, with pseudosiphon in outer dorsal wall; spur absent; inner dorsal lobe without palp and cleft; rhipidion present; shield absent; sentinel and spike simple and positioned laterally, with sentinel capable of rotation; two dT cartilages with dT_1 well developed; Ax simply-pointed; vT absent; aT_1 and aT_2 similar in shape with slightly pointed, blade-like distal ends.

As has been pointed out, Hulley (1972*a*) has made tentative suggestions regarding the phylogenetic position of the Anacanthobatidae. He has proposed an early origin for the family, deriving it from the hypothetical *Dipturus* ancestral stock. This would mean therefore that certain characters of the Anacanthobatidae would also be exhibited by the Crurirajidae, *Dipturus*, *Amblyraja*, *Rajella* and *Leucoraja* species (Hulley 1972*a*: fig. 56).

The presence of an erectile rhipidion in all anacanthobatids, as well as the retention of the well developed distal projection to the dM, in the form of the palp, in *Anacanthobatis foliorostris*, *A. marmoratus* and *A. longirostris* (Figs 4, 7; Hulley 1972*a*: fig. 10) would substantiate this theory. However, the distal projection of the dM is not well developed in *A. americanus* and *A. borneensis* (Fig. 12; Hulley 1972*a*: fig. 11), but the lack of a vT and dT_1 respectively in these species, indicates a somewhat specialized condition of the claspers. This specialization is further emphasized by the arrangement and number of dT cartilages in *A. americanus* (Hulley 1972*a*: fig. 44), and by the peculiar development of the anterior notch of the vT in *A. borneensis* (Fig. 11).

The Crurirajidae might be considered to be directly ancestral to the Anacanthobatidae, since both families are characterized by the anterior limb-like lobe of the pelvic fin, and the absence of dorsal fins would then appear as a progression away from the crurirajid condition. Furthermore, the attachment process of the aT_2 in *Anacanthobatis* could then be interpreted as a development from the terminal bridge in *Cruriraja* (Hulley 1972*a*: figs 40, 41, 42). This terminal bridge links the aT_2 with the Ax. However, the position of the dT_1, nature of the Ax and typical condition of the aT_1 and aT_2 in *Cruriraja* preclude a direct development of the Anacanthobatidae from this family. Furthermore, an attachment process to the aT_2 is also developed in the *Rajella/Leucoraja/Amblyraja* line of evolution (Hulley 1972*a*: fig. 26).

A relationship with the *Amblyraja/Rajella/Leucoraja* line is further exemplified by the well developed dT_3 (spur) in almost all anacanthobatids, a framework arrangement of the dT cartilages, the medial position of the anterior notch of the vT and the reduction in size of the dT_2. However, *Anacanthobatis* lacks the external pseudosiphon so typical of this group. The pseudosiphon in *Anacanthobatis americanus* (Hulley 1972*a*: fig. 11), although having a direct relationship with the dT_1, is not comparable to the form of this structure in *Amblyraja* and (?) *Rajella.*

To conclude, the Anacanthobatidae appear to have arisen separately from the same ancestral stock as both the Crurirajidae and the *Amblyraja/Rajella/Leucoraja* lines, and probably represent a direct modification of the *Dipturus* ancestral stock, which lost the pseudosiphon but retained the distal projection of the dM (palp) during the development of the rhipidion (Fig. 14). On the basis of clasper comparison therefore, the family does not now appear to have a diphyletic origin.

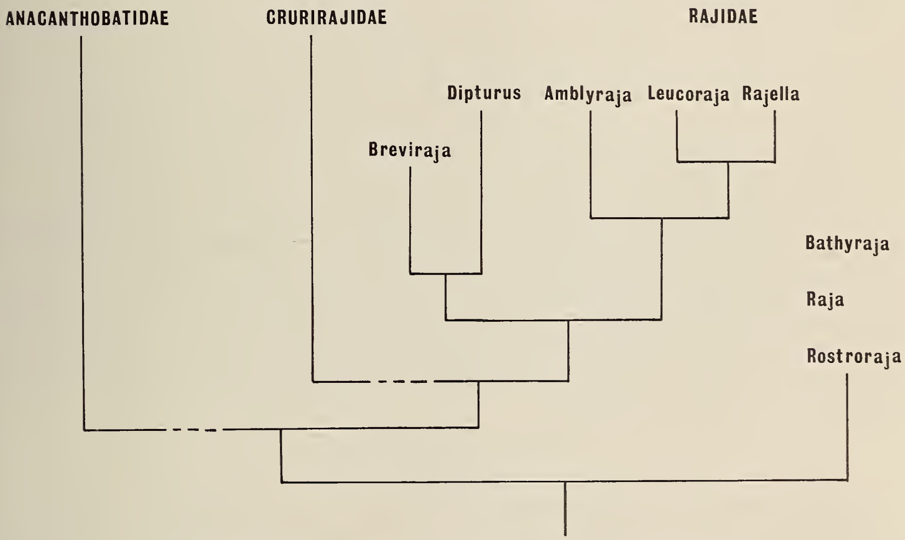

Fig. 14. Proposed phyletic relationships of the Anacanthobatidae.

Springeria probably represents the least specialized subgenus, closest to the basic ancestral stock, since the Ax is pointed, the distal end of the dM is well developed and the vT is relatively simple. Furthermore, the primitive condition of an elongate snout is retained, cf. *Dipturus* (Hulley 1972*a*). The anterior leaf-like expansion of the snout in *Anacanthobatis foliorostris* represents a direct modification of the condition in *A. longirostris* and would suggest a lesser age for *A. foliorostris*, a fact which is supported by the complete dorsal rotation of the dT_1.

The subgenus *Anacanthobatis* would then represent a split from the above condition, in which the snout was reduced, probably as an increased advantage in grubbing (Ishiyama 1958; Hulley 1972*a*). Further, there was a change in form of the Ax and vT cartilages. The presence of a spatulate Ax, together with the loss of the dT_4 might be interpreted as a condition arising from the pointed Ax/plate-like dT_4 typical of *Springeria*. The windowing of the vT may represent the initial stages leading to the reduction (e.g. *A. borneensis*) and complete loss (e.g. *A. americanus*) of the vT. However, the retention of the primitively pointed Ax in these species precludes a direct modification of *Sinobatis* and *Schroederobatis* from *Anacanthobatis*.

Rather the complete loss of the vT, dT_3 and dT_4 cartilages in *Schroederobatis* represents a specialized condition, which may be associated with the lateral shift in position of aT_1 and aT_2. This suggestion may be valid if we consider that essentially the clasper of the male skate plugs the cloaca of the female. In *Schroederobatis* the dT_1 does not show complete dorsal rotation and, as has been pointed out above, the Ax retains its pointed condition, facts which suggest a specialization of the condition in *Springeria*.

Similarly, *Sinobatis* would represent a specialized condition arising from *Springeria*: the Ax is pointed and the dT_3 is comparatively well developed, although it does not manifest itself as a spur in the glans. Again the loss of the dT_1 may be associated with the lateral shift in position of the aT_1 and aT_2 cartilages, together with the peculiar development of the anterior notch of the vT, which runs around the Ax stem on to the dorsal surface of the glans.

It has already been suggested (Hulley 1972*a*, *b*) that the Crurirajidae and *Breviraja* may have had their origin in the waters of the central western Atlantic and may have spread from this area to the southern African region at a later date. On the evidence presented above, this would also seem to be the case in the Anacanthobatidae, since not only are the most primitive forms known from the western central Atlantic but this region also shows the greatest species diversity of Anacanthobatidae.

Summary

The lectotype of *Anacanthobatis marmoratus* Von Bonde & Swart, 1923 is designated and described.

The pelvic girdles, rostral filaments, pectoral and pelvic radials of the Anacanthobatidae and the clasper structure of *Anacanthobatis longirostris*, *A. borneensis* and *Springeria foliorostris* are described.

On the basis of the above, it appears that the anterior leaf-like expansion of the snout is present only in *S. foliorostris* and is valid only as a diagnostic character at the species level. The genus *Springeria* is taxonomically invalid at the generic level, and all species should be referred to the genus *Anacanthobatis*. A key to the species is given.

Since there are relatively few species involved in the family Anacanthobatidae, further division into subgenera does not serve a useful taxonomic purpose. However, for interpretation of the phylogeny of the family, subgeneric groupings, based on the clasper structure, have been constructed as follows:

Family **Anacanthobatidae**

Genus *Anacanthobatis* Von Bonde & Swart, 1923
  type-species *Anacanthobatis marmoratus* Von Bonde & Swart, 1923

1. subgenus *Anacanthobatis* Von Bonde & Swart, 1923
   type-species *Anacanthobatis marmoratus* Von Bonde & Swart, 1923
   species: (?) *Anacanthobatis ori* (Wallace, 1967)
2. subgenus *Springeria* Bigelow & Schroeder, 1951
   type-species *Anacanthobatis foliorostris* (Bigelow & Schroeder, 1951)
   species: *Anacanthobatis longirostris* Bigelow & Schroeder, 1962
3. subgenus ***Sinobatis*** n. subgen.
   type-species *Anacanthobatis borneensis* Chan, 1965
   species: (?) *Anacanthobatis melanosomus* (Chan, 1965)
4. subgenus ***Schroederobatis*** n. subgen.
   type-species *Anacanthobatis americanus* Bigelow & Schroeder, 1962

In accordance with Article 67(k), of the International Code of Zoological Nomenclature, *Springeria* is retained as a subgenus, but is redefined.

The phyletic interrelationships of the family are discussed in terms of these morphological details and an evolutionary pattern is proposed. On this evidence it seems likely that, as in the case of the Crurirajidae and of *Breviraja*, the Anacanthobatidae had their origin in the central western Atlantic.

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